

FEEDING AND PREY SELECTION BY LARVAE OF *ENALLAGMA CYATHIGERUM* (CHARPENTIER) IN RELATION TO SIZE AND DENSITY OF PREY (ZYGOPTERA: COENAGRIONIDAE)

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When offered prey of 2 sizes, larvae of *E. cyathigerum* exhibited typical Type-II functional-response curves. When offered equal proportions of the two prey types, larvae preferred the larger type, regardless of hunger level. When offered different relative proportions of the two prey types, larvae markedly preferred the large type, except when the latter were least numerous. We interpret our findings in the light of classical optimal diet theory.

INTRODUCTION

The ways in which dragonfly larvae react to their prey constitute a key element in attempts to understand the trophic structure of animal communities in fresh water (MACAN, 1977; JOHNSON & CROWLEY, 1980) as well as determining the feasibility of using such larvae as agents in biological-control programmes. Among the aspects of predatory behaviour so far studied in the laboratory have been the numerical (CROWLEY, 1975) and functional responses (THOMPSON, 1975, 1978a; KHORKHODIN, 1985) to prey and the selection of prey according to species, when presented at different densities, including the phenomenon of "switching" — namely the supraproportional consumption of whichever of 2 prey items is the more abundant (see LAWTON et al., 1974; AKRE & JOHNSON, 1979; CROWLEY, 1979; COLTON, 1987). Studies of size preference for prey in the field support the conclusion that no selection for prey size occurs within the size-range of organisms that dragonfly larvae can capture; for example larger larvae of *Ischnura elegans* (Vander Linden) consume a wider range of prey size than do smaller larvae although the minimum size of

prey they take remains much the same (THOMPSON, 1978b). In laboratory studies of size preference, large and small prey have usually belonged to different species (e.g. CROWLEY, 1979; CHOWDHURY & RAHMAN, 1984; COLTON, 1987); apparently few authors have yet investigated size preference using large and small prey of the same species, although to do so tests more rigorously the hypothesis that size *per se* influences choice of prey. An exception is the work of BLOIS (1982) who offered larvae of *Anax imperator* Leach two different sizes of *Daphnia magna* over a range of absolute and relative densities: larvae of the final (F-0) and penultimate (F-1) instars preferred large prey when the overall density of prey was high, and F-2 and F-3 larvae preferred large prey at all absolute densities but were more selective when absolute densities were high. Here we report the results of a preliminary investigation of a similar kind and characterize some effects on size preference of density and proportional abundance of 2 sizes of prey. We take the opportunity to interpret our results in terms of contemporary foraging theory (e.g. STEPHENS & KREBS, 1986). The species investigated is *Enallagma cyathigerum* (Charpentier), a coenagrionid similar in size to *I. elegans*, the species studied by LAWTON et al. (1974) and THOMPSON (1975).

MATERIAL AND METHODS

Larvae of *E. cyathigerum* were collected by handnet from Rohallion Loch, Perthshire (56°32'N, 3°32'W; NO 048 387) during October 1986. They were identified using characters described by CHOWDHURY & CORBET (1987). In all experiments 2 sizes of larvae were used, their body lengths (excluding antennae and caudal lamellae) being 9-10 mm ("small") and 15-17 mm ("large", comprising F-1 and F-0 instars). After collection, each larva was held in a separate container in a cabinet at $15 \pm 1^\circ\text{C}$ under an artificial photoperiod of 12 h. All experiments were conducted in the laboratory at 18-20° C and during daytime under an unregulated, artificial photoperiod; for 2 days before an experiment larvae were held under laboratory conditions for acclimatisation. Because feeding ceases at a late stage of metamorphosis, we need to state here that no larva showed external signs of metamorphosis (CORBET & PROSSER, 1986) when collected. Larvae were not again inspected to detect such signs, but we can confidently assume that no larva, during an experiment, had reached a stage of metamorphosis sufficiently advanced for its feeding to be affected: had this been so the conspicuous swelling of the wing-sheaths would have been noticed.

Experimental containers (each accommodating 1 dragonfly larva and its prey) were white, opaque, plastic, circular tubs (diameter of top and bottom 8.2 and 6.6 cm, height 5.5 cm) containing 100 ml of tapwater (depth 3.0 cm). Prey larvae of the mosquito, *Aedes aegypti* (L.) of two sizes: 1-day old ("small", comprising instars II (mainly) and I, body lengths ca. 3.0 and 1.7 mm; wet weights ca. 0.24 and 0.05 mg) and 5-days old ("large", comprising instar IV, length ca. 6.5 mm; wet weight ca. 3.4 mg). The observation period for each experiment was 30 min. No dragonfly was used more than once in any one of these three sets of experiments or in any one replicate within an experiment; but the same individual larva could have been used again in a different experiment.

Experiments were designed to answer 3 questions for both small and large dragonfly larvae. These questions (and the measure of performance used to answer them) were as follows:

Experiment 1: What are the functional response curves, the rates of search and the handling times? (Numbers of prey consumed at different densities of prey.)

Experiment 2: Is a preference shown for small or large prey and, if so, is it affected by the predator's hunger level? (Numbers of small and large prey consumed when both sizes of prey are continuously provided in equal numbers and when hunger level of predator varies.)

Experiment 3: If so, does such a preference depend on the relative densities of small and large prey and, if it does, does "switching" between prey sizes occur? (Numbers of small and large prey consumed when both sizes of prey are provided initially at several complementary densities.) Arrangements peculiar to each experiment are described below.

EXPERIMENT 1 — Dragonfly larvae were denied food for 24 h before the experiment began. Prey larvae were provided, once only, at the beginning of each experiment at each of 5 densities per predator: 2, 4, 8, 16 and 32. At the end of the experiment the numbers of prey consumed were recorded. Each treatment was replicated 5, 6 or 7 times. Rates of search and handling times were estimated from the data using ROGERS' (1972) random predator equation by the technique of non-linear least-squares regression:

$$N_a = N(1 - \exp(-a(T-bN_a)))$$

where N_a = the number eaten, N = initial prey density, a = rate of search, b = handling time and T = duration of experiment. The parameters "rate of search" and "handling time" are defined in this context by ROGERS (1972) and our abbreviations in this paper follow HUBBARD et al. (1982).

EXPERIMENT 2 — Dragonfly larvae were denied food for 24, 48 or 96 h before the experiment began. Ten prey larvae of each size were provided at the beginning of each experiment; this density (10 prey of each size) was kept constant throughout the experiment by observing each predator continuously and replacing immediately (i.e. within 10 sec) each prey larva eaten with one of the same size. The numbers of prey consumed, as well as the sequence in which small and large prey were consumed, were recorded. Each treatment was replicated 5 times.

EXPERIMENT 3 — Dragonfly larvae were denied food for 24 h before the experiment began. Fifty prey larvae were provided at the beginning of each experiment, small and large larvae (respectively) being present in the following proportions in the 9 treatments: 1:9, 2:8, 3:7, 4:6, 5:5, 6:4, 7:3, 8:2 and 9:1. At the end of the experiment the numbers of prey consumed were recorded. Each treatment was replicated 6 times.

RESULTS

EXPERIMENT 1

The functional response curves for 2 sizes of dragonfly larvae and 2 sizes of prey, and the corresponding calculated values for rate of search (a) and handling time (b) are shown in Figure 1. In Figure 1a for small prey the small numbers of prey consumed at the highest density reduce the correspondence between observed and expected values. In Figure 1a for large prey the relatively poor correspondence is caused by high consumption at the two lowest densities of prey. In Figure 1b for small prey there is negligible difference between observed and expected values; and values for a and b are much higher than for small predators offered small prey (Fig. 1a). In Figure 1b for large prey consumption declines at the

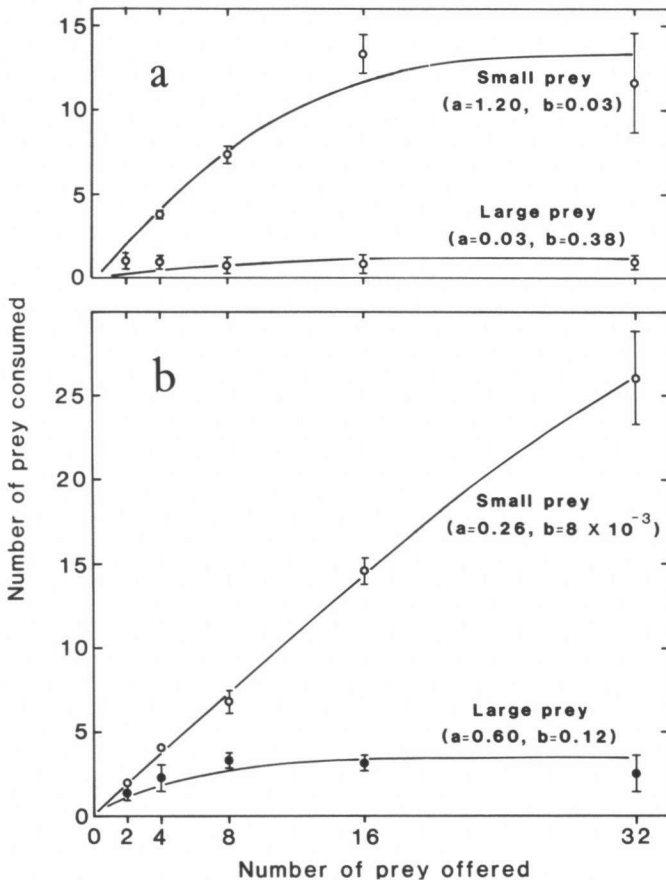


Fig. 1. Functional-response curves for *E. cyathigerum* larvae offered *Aedes aegypti* larvae as prey: (a) small predators; (b) large predators. Number of replicates: small predator, small prey — 5; small predator, large prey — 5; large predator, small prey — 6; large predator, large prey — 7. For each result the estimate for rate of search (a) and handling time (b) are shown. Units of a are $l\ h^{-1}$ and b are h. A vertical bar shows the standard error of the mean. Solid lines join values predicted from ROGERS' (1972) model.

two highest densities of prey, producing a negative value for handling time ($a = 3.00 \times 10^{-4} l\ h^{-1}$; $b = -17.5\ h$). Although this gives the best fit to the data, it is biologically meaningless; so alternative values for a and b (as given in Fig. 1b) have been obtained by omitting from the calculation the results for the highest density of prey. Having regard to the physical interference to the predator probably caused by such a high density of (large) prey, such an omission may give more realistic values for a and b.

EXPERIMENT 2

The results are shown in Table I. All but one of the predators consumed an unbroken sequence of either small or large prey larvae, the exception being the 1 small predator at 96 h: it consumed 1 small prey and then 1 large one. Significantly more predators of both sizes, and especially large predators, took only large prey (for small predators $\chi^2 = 7.14$ for which $0.01 > P > 0.005$; for large predators $\chi^2 = 14.0$ for which $P < 0.001$). More replicates might reveal that the difference in preference shown by small and large predators is significant. Noteworthy was the small predator at 48 h which, despite the significant preference for large prey shown by small and large predators, consumed 9 prey larvae all of which were small. No correlation can be detected between the hunger level of the predator and either the number or size of the prey consumed.

TABLE I

EXPERIMENT 2. Prey consumption by *E. cyathigerum* when offered a choice between small and large prey and when denied food beforehand for different periods (N = 5 for each treatment)

Period (h) during which food was denied before experiment	Number of prey eaten and (numbers of predators feeding)		
	Small prey	Large prey	Totals
Small predators			
24	2 (1)	5 (4)	7 (5)
48	9 (1)	5 (4)	14 (5)
96	1 (1)	9 (5)	10 (5) ¹
Totals	12 (3)	19 (13)	31 (15) ¹
Large predators			
24	0 (0)	18 (4)	18 (4)
48	0 (0)	23 (5)	23 (5)
96	0 (0)	21 (5)	21 (5)
Totals	0 (0)	62 (14)	62 (14)

¹ Only 5 predators fed, one taking both small and large prey.

EXPERIMENT 3

Figure 2 shows that the preference for large prey is evident at all the complementary densities of small and large prey to which the predator was exposed and that this preference is less marked when large prey are less numerous.

DISCUSSION

Our results show that *E. cyathigerum* larvae show a Type-II functional response typical of invertebrate predators. When presented with a choice between

large and small prey, *E. cyathigerum* preferred large prey except when they were present at a low density. Preference for large prey was unaffected by predator hunger level — at least within the range tested.

In Experiment 1 the low consumption of prey at the highest prey density may have been due to physical interference with feeding caused by a large number of large prey. Because the relative sizes of predator and prey may vary in experiments of this kind, as will the absolute size and activity of prey, one must be prepared for departures from an expectation derived from a general theoretical model which, by its nature, cannot take into account size- and species-specific behaviour related to activity or size.

In recent years much attention has focused on the decisions that predators should make while foraging if they are to maximise their rate of energy intake, the rationale for this being that

individuals with higher rates of energy intake will have greater fitness (KREBS & McCLEERY, 1984; STEPHENS & KREBS, 1986). CHARNOV (1976) developed a simple model for situations in which a predator is presented with a choice between prey items of different type. This model is often referred to as the "classical optimal diet model" (e.g. KREBS & McCLEERY, 1984). The predictions of the model are as follows. Predators should rank prey items on the basis of the *profitability* of prey items. Profitability is defined as E_i/b_i where E_i is

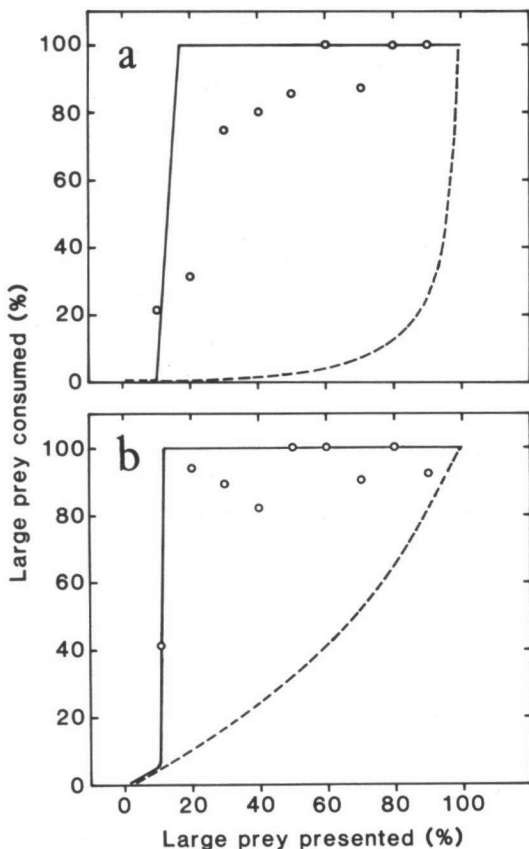


Fig. 2. Proportion of large prey consumed by small (a) and large (b) *E. cyathigerum* larvae when presented with small and large prey larvae in differing proportions. Solid lines show predictions derived from CHARNOV's (1976) classical optimal diet model. Broken lines show the predictions of the extended (2-prey) version of ROGERS' (1972) random predator equation.

the energetic content of prey type i and b_i is the handling time for prey type i . The predator should always eat the most profitable prey type (i.e. that gives the highest value of E_i/b_i). If the predator is presented with a choice between two prey items, one more profitable than the other, the predator should take the more profitable prey type alone when:

$$\frac{a_i N_i E_i}{1 + a_i N_i b_i} > \frac{a_i N_i E_i + a_j N_j E_j}{1 + a_i N_i b_i + a_j N_j b_j} \dots\dots\dots (1)$$

Where:

a_i, a_j = rate of search for prey types i and j ;
 b_i, b_j = handling time for prey types i and j ;
 E_i, E_j = energetic content of prey types i and j ; and
 N_i, N_j = densities of prey types i and j .

That is to say, predators should take only the more profitable prey type when the rate of energy intake by doing so (given by the left hand side of the inequality is greater than when both prey types are taken (the right hand side of the inequality).

Inequality (1) is satisfied by values of N_i as follows:

$$N_i > \frac{E_j}{a_i(E_i b_j - E_j b_i)}$$

Therefore there is a critical density \hat{N}_i above which the predator should take only the more profitable of the two prey types. \hat{N}_i can be calculated as follows:

$$\hat{N}_i = \frac{E_j}{a_i(E_i b_j - E_j b_i)}$$

Note that \hat{N}_i is independent of N_j , the density of the less profitable prey.

S. Jordan (unpublished) determined the energetic content of *A. aegypti* which had been reared under conditions very similar to those used in the experiments described here. Average calorific values were: instar II — 0.429 J; instar IV — 10.2 J. Profitabilities can be calculated by dividing the calorific content of each prey type by the appropriate handling time. For small predators profitabilities are therefore 12.7 J h⁻¹ and 26.9 J h⁻¹ for small and large prey. For large predators the corresponding values are 53.7 J h⁻¹ and 82.0 J h⁻¹. Therefore, large prey are the more profitable for both large and small predators. Using values of a_i, a_j, b_i and b_j derived from Experiment 1, it is possible to calculate values of \hat{N}_i for large and small predators. These were 57.9 prey per litre for large predators and 82.3 prey per litre for small predators.

HUBBARD et al. (1982) point out that if one wishes to predict the pattern of prey selection which will be produced by an animal foraging in a manner that is consistent with Charnov's optimal diet model, exploitation of the prey popu-

lations must be taken into account. It is possible that at the start of an experiment the density of the more profitable prey is above \hat{N}_i , but that as the predator exploits this prey type it reduces the density to below \hat{N}_i . When the predator has done this it should change its behaviour and take both prey types. Exploitation before \hat{N}_i is reached can be described by ROGERS' (1972) random predator equation, because only one prey type is taken. For the remaining period of the experiment extended versions of the random predator equation can be used to predict number of prey taken:

$$N_{ai} = N_i(1 - \exp(-a_i(T - b_i N_{ai} - b_j N_{aj})))$$

$$N_{aj} = N_j(1 - \exp(-a_j(T - b_j N_{aj} - b_i N_{ai})))$$

Where:

N_{ai} , N_{aj} = number of prey types i , j eaten.

Using these equations it is possible to predict the proportion of each prey type in the predator's diet after the 30-minute experimental period. These predictions are shown in Figure 2. Also shown are the predictions of the two-prey version of the random predator equations, assuming that the predator takes both prey types throughout the experiment. Clearly, the optimal diet model provides a better fit to the predator's behaviour than does the extended random predator equation. For both sizes of *E. cyathigerum* larvae, the diet only comprised a large proportion (> 50%) of small prey at densities approximately equal to \hat{N}_i (5/45 for large predators; 5/45 and 10/40 for small predators). The model predicts that the diet of large predators undergoing the 8 treatments with the highest density of large prey should consist entirely of large prey. This was the case in only three of the prey combinations offered; in the other treatment a few small (less profitable) larvae were taken. Similar results were found for small predators. Thus, whereas the model gave a good qualitative prediction of predator behaviour, it did not give a precise quantitative prediction.

It might be argued that, because *E. cyathigerum* and *A. aegypti* have a negligible history of coevolution (limited, perhaps to the duration of this study), that to expect a fit between an optimal foraging model and the behaviour of *E. cyathigerum* is naive. However, zygopteran larvae such as *E. cyathigerum* feed on a wide variety of small arthropods, such as chironomid larvae, which are similar to mosquito larvae. Much research has shown that, when foraging, animals may use simple criteria, or "rules of thumb", which enable their behaviour to approximate to the optimal behaviour (cf. STEPHENS & KREBS, 1986, p. 172). For example, BARNARD & BROWN (1981) showed that the Common Shrew, *Sorex araneus* L., does not assess E/b directly, but uses the size of a prey item as a measure of profitability. We suggest that dragonfly larvae may use size to assess profitability in a similar way. For a polyphagous aquatic predator which has a

relatively long period of larval development and so will experience a wide variety of different types of food through the march of the seasons, assessment of profitability by some simple rule of thumb, such as size, may well be an efficient way of foraging so as to approach a maximum rate of energy intake.

AKRE & JOHNSON (1979), BLOIS (1982) and COLTON (1987) found that dragonfly larvae exhibited frequency-independent preference for one of two prey types. In addition, AKRE & JOHNSON (1979) and BLOIS (1982) found that preference increased with prey density. Evidence for frequency-dependent preferences (apostatic selection, or switching) was presented by LAWTON et al. (1974) and AKRE & JOHNSON (1979). In contrast, BLOIS (1982), BERGELSON (1985) and COLTON (1987) found no evidence of frequency-dependent selection.

BLOIS (1982) and BERGELSON (1985) investigated the behavioural mechanisms which produced prey selection in *Anax*. Prey capture consists of a sequence of behaviours in which orientation to a prey item is followed by pursuit and then capture. BLOIS (1982) showed that selection occurs because the predators orientate preferentially towards the preferred prey item, whereas BERGELSON (1985) found that increased probability of pursuit of one prey type resulted in selective predation. A different hypothesis was proposed by AKRE & JOHNSON (1979) to account for switching by larvae of *Anomalagrion hastatum* (Say) larvae. Predators in this study were offered two species of cladoceran: *Daphnia*, a relatively active swimmer, and the less active *Simocephalus*. The authors suggested that when *Daphnia* were more abundant predators could forage efficiently by adopting a "sit-and-wait" strategy, but that when *Simocephalus* were the more abundant prey type, the predators changed to an active foraging strategy.

Few studies have considered the adaptive significance of observed patterns of prey selection. BERGELSON (1985) showed that the success of a larva of *Anax junius* (Drury), in capturing a particular type of prey item increased with the number of times it pursued that type of prey item; so one might expect the predator to devote its feeding efforts to the most abundant prey type, since it would enjoy an increased probability of successful capture by doing so. Our study, in contrast to some previous studies (AKRE & JOHNSON, 1979; BLOIS, 1982; BERGELSON, 1985), shows that classical optimal diet models can be used to predict, at least in a qualitative way, prey selection by dragonfly larvae. Further, our results are consistent with the notion that patterns of prey selection by *E. cyathigerum* larvae function in a way that tends to maximise the predator's rate of energy intake. That the behaviour of our larvae provided only a qualitative fit should not be seen as a reason for rejecting the study of dragonfly prey preference based on optimality theory. In particular, data rarely support the prediction that the less profitable prey is excluded from the diet when the density of the more profitable prey is greater than \hat{N}_j . There are various explanations of

such "partial" preferences (see McCLEERY & KREBS, 1984, pp. 98-99). Such deviations of observed behaviour from model predictions offer opportunities to test new hypotheses about prey-selection behaviour and do not necessarily invalidate the optimality approach.

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